ARTICLE

Status and Conservation of Interior Redband Trout in the Western United States

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Abstract
    In this article we describe the current status and conservation of interior (potamodromous) Redband Trout *Oncorhynchus mykiss* sspp. throughout its range in the western United States using extant data and expert opinion provided by fish managers. Redband Trout historically occupied 60,295 km of stream habitat and 152 natural lakes. Currently, Redband Trout occupy 25,417 km of stream habitat (42% of their historical range) and 124 lakes or reservoirs. Nonhybridized populations are assumed to occupy 11,695 km (46%) of currently occupied streams; however, fish from only 4,473 km (18%) have been genetically tested. Approximately 47% of the streams occupied by Redband Trout occur on private land, 45% on government lands, and 8% in protected areas. A total of 210 Redband Trout populations, occupying 15,252 km of stream habitat (60% of the current distribution) and 95,158 ha of lake habitat (52%), are being managed as "conservation populations." Most conservation populations have been designated as weakly to strongly connected metapopulations (125; 60%) and occupy much more stream length (14,112 km; 93%) than isolated conservation populations (1,141 km; 7%). The primary threats to Redband Trout include invasive species, habitat degradation and fragmentation, and climate change. Although the historical distribution of interior Redband Trout has declined dramatically, we conclude that the species is not currently at imminent risk of extinction because it is still widely distributed with many populations isolated by physical barriers and active conservation efforts are occurring for many populations. However, the hybridization status of many populations has not been well quantified, and introgression may be more prevalent than documented here. We recommend (1) collecting additional genetic data and estimating distribution and abundance by means of a more rigorous spatial sampling design to reduce uncertainties, (2) collecting additional information to assess and predict

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the impacts of climate on populations, and (3) continuing to use this database to evaluate the status of Redband Trout and inform conservation efforts through time.

Rainbow Trout *Oncorhynchus mykiss* are one of the most widely distributed and diverse groups of native salmonids in western North America. Although the taxonomic nomenclature for this species remains unresolved, patterns of genetic diversity show major genetic differences between coastal and inland groups, representing major phylogenetic divisions within the species and among inland groups (Allendorf 1975; Behnke 1992; Stearley and Smith 1993; Currens et al. 2007, 2009; Blankenship et al. 2011; Pearse et al. 2011). Native Rainbow Trout occurring west of the Cascade Range and the Sierra Nevada are currently classified as coastal Rainbow Trout *O. mykiss irideus*, whereas Rainbow Trout occurring east of these mountain ranges are classified as Redband Trout. Behnke (1992) identified three subspecies of Redband Trout: (1) Columbia River Redband Trout *O. mykiss gairdneri*, which occur in the Columbia and Fraser rivers; (2) northern Great Basin and Upper Klamath Lake Redband Trout *O. mykiss newberrii*; and (3) Sacramento Redband Trout *O. mykiss stonei*, which occur in the Pit and McCloud rivers. Similarly, Currens et al. (2009) found the greatest evolutionary divergence among Redband Trout groups in three major river basins: the upper Sacramento, Klamath, and Columbia rivers. Currens et al. (2007) suggested that Redband Trout be segregated into at least four groups: (1) Columbia River populations, *O. mykiss gairdneri*; (2) populations from Goose Lake, the Warner Lakes, and the Chewaucan Basin, which are evolutionarily closest to *O. mykiss stonei*; (3) populations from Upper Klamath Lake and the upper Klamath River (the type location of *O. mykiss newberrii*), and (4) an unnamed subspecies in the headwaters of the upper Klamath basin and coastal Klamath Mountain populations. Populations from other isolated pluvial lake basins in Oregon appear to be evolutionarily closest to *O. mykiss gairdneri* or could not be unambiguously assigned to one of the above groups. Genetic and morphological data suggest that these major evolutionary groups warrant subspecies recognition (Allendorf 1975; Berg 1987; Behnke 1992; Stearley and Smith 1993; Currens et al. 2009).

Redband Trout have persisted for millennia in a dynamic landscape that has undergone tremendous geological and hydrological changes from volcanism, continental glaciation, periodic major flooding associated with glacial Lake Missoula, and the formation and desiccation of large pluvial lakes (Currens et al. 2009). Their historical distribution spans six states in the United States (Nevada, California, Oregon, Washington, Idaho, and Montana) and encompasses a wide array of habitats, ranging from the Finlay River drainage in northern British Columbia, south to desert streams in arid regions of northeastern California and northern Nevada and pluvial lake basins in

Oregon (hereafter, Closed Oregon Basins), and east to montane streams in the headwaters of the Columbia River drainage in Montana and Idaho. Differences in climatic regimes and habitat conditions across this broad geographic area are reflected in the patterns of genetic diversity (Blankenship et al. 2011) and likely resulted in the adaptation of Redband Trout populations to differing local environments (Narum et al. 2010, 2013). For example, many desert populations exhibit physiological tolerances to elevated stream temperatures and intermittent flows (Gamperl et al. 2002; Rodnick et al. 2004; Cassinelli and Moffitt 2010; Narum et al. 2010), and some populations in the upper Klamath and Columbia River basins appear to be resistant to infection from *Ceratomyxa shasta*, a myxosporean parasite that infects salmonids (Buchanan et al. 1983; Currens 1997; Atkinson and Bartholomew 2010).

Redband Trout exhibit two major life histories, anadromous (steelhead) and potamodromous. Potamodromous Redband Trout exhibit a wide variety of life history strategies in freshwater systems, including migratory (i.e., fluvial and adfluvial) and resident forms. Adfluvial Redband Trout migrate from lakes to tributaries for spawning and rearing, a good example being the Kamloops Rainbow Trout (Gerrards) of Kootenay Lake, British Columbia. Fluvial Redband Trout occupy large rivers and spawn in smaller tributaries. Resident forms inhabit smaller tributaries and headwater areas for their entire lives. In this paper, we confine our analysis to potamodromous Redband Trout populations that are outside the current range of steelhead (hereafter referred to as interior Redband Trout), relying on the knowledge of barriers to anadromy to define the potential range for the allopatric form (Thurow et al. 1997).

Over the past century, many populations of Redband Trout have experienced large reductions in their distribution relative to their historically occupied habitats, primarily owing to habitat degradation, habitat fragmentation, and nonnative species introductions (Williams et al. 1989; Thurow et al. 1997, 2007). Widespread introductions of nonnative salmonids, primarily coastal Rainbow Trout, eastern Brook Trout *Salvelinus fontinalis*, and Cutthroat Trout *O. clarkii* sspp., have been especially detrimental to native populations because of intensive competition and widespread hybridization (Behnke 1992). As a result of declines in distribution, abundance, and genetic diversity, the interior Redband Trout is currently considered a species of special concern by the American Fisheries Society (Williams et al. 1989) and the U.S. Fish and Wildlife Service in most states in the historical range and is classified as a sensitive species by the U.S. Forest Service and Bureau of Land Management. In 1994, the Kootenai River Redband Trout in northern Idaho was petitioned for listing under the

U.S. Endangered Species Act (ESA), but the petition was dismissed because there was insufficient information with which to identify the Kootenai River population as a distinct population segment. A petition was also made for the Redband Trout populations occupying the Catlow, Fort Rock, Harney, Warner Lakes, Goose Lake, and Chewaucan basins of eastern Oregon in 1997, but this petition too was denied. Concerns about the persistence of steelhead populations in the interior Columbia River basin have resulted in several listings under the ESA. However, potamodromous forms were not included in the final listings because there was insufficient information about the distinction between steelhead and resident Redband Trout. As a result, only the anadromous form (and, by coincidence, sympatric resident populations) receive direct protection and benefits from conservation planning under the ESA. Because of the exclusion of potamodromous populations, there was strong impetus for state, federal, tribal, and nongovernmental agencies to conduct a consistent and comprehensive rangewide status assessment for interior Redband Trout to inform conservation management and recovery programs.

Thurow et al. (2007) published an initial review of the historical and current distributions and status of Redband Trout (circa 1996) in the U.S. portion of the interior Columbia River basin and portions of the Klamath River and Great Basins. Their assessment considered (1) Redband Trout that evolved in sympatry with steelhead and (2) allopatric forms that evolved outside the historical range of steelhead, and it used data compiled from surveys and the expert opinions of biologists at a subwatershed scale. During the past 16 years, a substantial amount of new information on the distribution and status of Redband Trout has emerged across their current range in the United States. More data are now available, and usually at a much finer spatial resolution (i.e., the reach-level hydrologic scale) than that used by Thurow et al. (2007) in their review. However, prior to our work these data had not been synthesized into a comprehensive review. Therefore, in 2012 we convened teams of fisheries professionals representing state, federal, and tribal agencies as well as nongovernmental organizations in a series of workshops to conduct a consistent and comprehensive rangewide status assessment for interior Redband Trout in the United States. The information derived from these workshops was compiled to identify the historically occupied range, current distribution, and genetic status and to assess risks for resident Redband Trout throughout their current range.

In this article, we provide a rangewide status assessment for interior Redband Trout in the United States using extant data and expert opinion. Our objectives were to (1) estimate the historical (circa 1800) distribution of interior Redband Trout outside the current range of steelhead; (2) determine the current distribution of interior Redband Trout using a spatially explicit analysis; (3) identify populations that managers are currently conserving; and (4) evaluate the threats to these populations. The overall goal of this review is to provide consistent and current information on the status of and conservation efforts for interior Redband Trout that will help managers conserve these fish.

AREA OF ANALYSIS

The area of analysis included the likely historical range (circa 1800) of interior Redband Trout occurring in major river basins of the United States that do not support anadromous fishes (Figure 1), including the middle and upper Columbia River basins, the Kootenai–Pend Oreille–Spokane basin, the Snake River basin, the Oregon Closed Basins, the Klamath–northern California coast basins, the Sacramento basin, and the north Lahontan basin. The assessment did not include the Canadian portions of the Redband Trout distribution, with the exception of a few streams that flow from the United States into Canada and then back into the United States. The information was partitioned into and is reported by 4th-level (8-digit) hydrologic units (HUCs).

METHODS[1]

In the winter of 2012, we convened 93 fisheries professionals from state, federal, and tribal agencies and nongovernmental organizations in 13 regional workshops to compile information on interior Redband Trout. Additionally, 15 geographical information system (GIS) and data management specialists participated in the workshops to facilitate the entry, display, and verification of data. Data at the stream-reach scale were entered into a GIS database using ArcGIS (version 10.0) and compiled by 4th-level HUCs using the 1:24,000 scale National Hydrography Dataset (NHD) as the basis for storing hydrographical and Redband Trout attribute information. A total of 69 4th-field HUCs were attributed and analyzed, each completed in "real time" during the workshop to which it was assigned. Standardized data protocols were modeled after those established for several other inland trout species (May et al. 2003; May and Albeke 2005; Shepard et al. 2005), commonly referred to as the Inland Cutthroat Trout Protocol (ICP), and were consistently applied by all workshop participants under the guidance of a common workshop facilitator. As of 2014, the database is housed at the Washington Department of Fish and Wildlife and may be accessed through a formal request.

The information used for the assessment was primarily empirical in nature but based on both sampled data and the professional judgment of field biologists (Table 1; see the Supplement in the online version of this article for details). Information sources were identified and linked to ranked levels of reliability to qualify information quality (May and Albeke 2005). Information associated with judgment calls and

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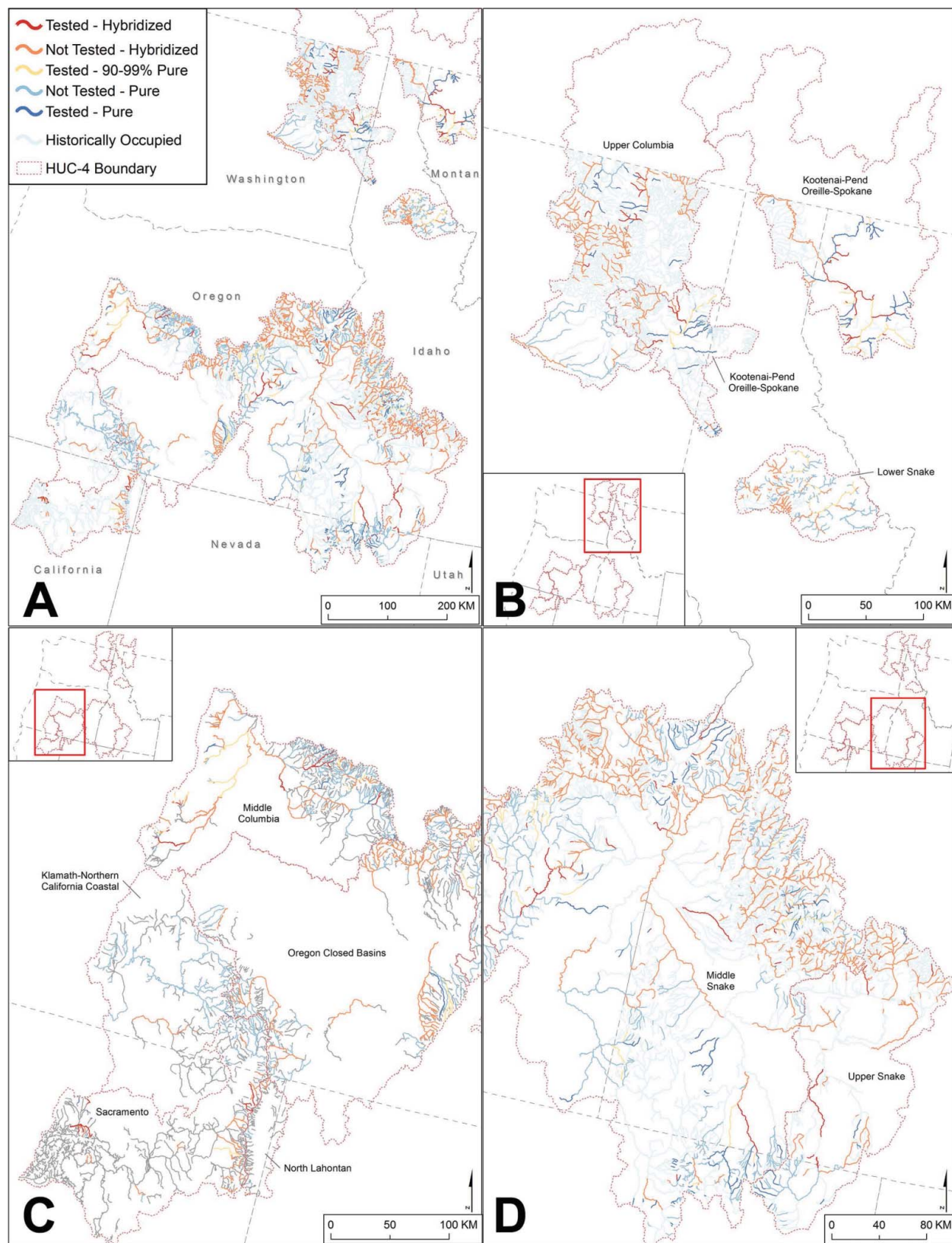[1]An extensive supplement to this article is available in the online version.

FIGURE 1.   Map delineating the distribution of interior Redband Trout **(A)** throughout their range and **(B)–(D)** in major geographic regions in the western United States. The colored lines indicate the estimated historical range and genetic status (see legend). [Color figure available online.]

TABLE 1. Kilometers of streams and rivers occupied (number of individual segments in parentheses) by major river basin and types of information sources used to estimate the current distribution of interior Redband Trout in the western United States.

River basin	Information source							
	Anecdotal	Professional judgment or ocular	Minor sampling	Major sampling	Unknown	Percent of empirical	Stream length (km)	Percent of total
Kootenai–Pend Oreille–Spokane	157 (9)	1 (0)	831 (46)	756 (42)	43 (2)	89	1,789	7.0
Upper Columbia	3 (0)	8 (0)	66 (3)	151 (7)	1,885 (89)	10	2,114	8.3
Upper Snake	72 (5)	0	1,018 (66)	383 (25)	80 (5)	90	1,553	6.1
Middle Snake	701 (6)	206 (2)	4,358 (37)	1,907 (16)	4,627 (39)	53	11,800	46.4
Lower Snake	130 (10)	0	945 (74)	81 (6)	123 (10)	80	1,279	5.0
Middle Columbia	955 (41)	186 (8)	1,016 (44)	121 (5)	27 (1)	49	2,306	9.1
Oregon Closed Basins	879 (34)	134 (5)	945 (36)	513 (20)	142 (5)	56	2,613	10.3
Klamath–northern California coast	11 (1)	168 (16)	726 (68)	154 (14)	4	83	1,062	4.2
Sacramento	67 (8)	14 (2)	586 (69)	0	176 (21)	69	843	3.3
North Lahontan	11 (18)	0	2 (4)	0	44 (77)	4	57	0.2

anecdotal sources was viewed as less reliable than information obtained via sampling surveys and studies that had undergone analysis and review. As in other applications of this approach, this assessment relied on existing information, and therefore sampling was not random and in many cases not spatially independent. As a result, there are undoubtedly biases inherent in the information.

Barriers.—Fish passage barriers were identified as locations (specific points) on the NHD stream layer and attributed within the ICP database. Barriers of historical significance were coded differently from barriers identified as only influencing the current distributions of Redband Trout. Historical barriers were primarily waterfalls and high-gradient cascading stream sections that would have prevented the invasion of upstream reaches by Redband Trout. Contemporary barriers include anthropogenic features such as culverts, dams, water diversions, and other features that were judged to have a significant influence on Redband Trout movement.

Historical and current distributions.—The estimated historical distribution of Redband Trout at the time of European expansion into the western United States (circa 1800) was based on four factors: (1) the known geological barriers to fish movement; (2) the physical and hydrologic ability of a stream to support Redband Trout; (3) historical accounts; and (4) recent information on Redband Trout occurrence. The primary determinant of the historical distribution of Redband Trout was the presence of geological features (e.g., waterfalls and high-gradient cascade stream segments) that would have precluded fish occupancy above a specific point. In other instances, habitat limitations such as small stream size, high stream gradient, and insufficient streamflow were judged to have limited the historical distribution. In some cases, historical determinations were based on specific information (e.g., historical

journals, diaries, natural history reports, and other historical documents).

We delineated the current distribution of Redband Trout using site-, reach-, stream-, and lake-specific information and professional judgment as to the presence of Redband Trout. Only wild, self-sustaining populations of Redband Trout were included in the analysis. The spatial resolution of the information varied. Consequently, site information was sometimes expanded to entire streams and in other cases was applied to specific stream reaches. A standard set of population and habitat characterizations, including genetic status, fish stocking, the presence of nonnative fish species, Redband Trout density, habitat quality, and life history forms (resident, fluvial, and adfluvial; see the Supplement for details) was made for each stream or stream reach (segment) and lake. Each currently occupied lake was treated as a single independent habitat segment.

The NHD data set was created in a consistent and structured manner (http://nationalmap.gov/standards/nhdstds.html). However, due to differences in geographic and ecological location and/or individual differences between personnel and base data, there may be some variability between the lengths of the individual stream reaches (termed the "ReachCode" level in the NHD database) within each 4-level HUC. We assessed the relative sensitivity of the occupancy data to the variation in reach lengths inherent in the NHD and the potential differences associated with different groups of professionals (i.e., attendees at the regional workshops) using a bootstrapped resampling approach in which several different proportional subsamples of both currently and historically occupied habitats were selected. We created an algorithm within Program R (R Development Core Team 2013) that randomly selected, without replacement, a set of stream reaches

from the available 4-digit HUC data sets and then calculated the proportion of historical habitat currently occupied by Redband Trout. This process was repeated for 1,000 iterations for nine different levels of subsampling (from 10% to 90% of the data in 10% intervals) of all historically occupied stream reaches. Means and 95% confidence intervals were estimated for the proportion of currently occupied habitats, assuming a normal distribution.

Fish stocking and the presence of nonnative fish species.— Available records of fish stocking and species surveys were reviewed and the resulting information was included for each stream segment or lake in the current distribution of Redband Trout. The focus of this review was on nonnative fish species that have the potential to hybridize or compete with native Redband Trout, including Coastal Rainbow Trout, Brown Trout *Salmo trutta*, Brook Trout, Lake Trout *Salvelinus namaycush*, native Westslope Cutthroat Trout *O. clarkii lewisi*, other subspecies of Cutthroat Trout, and several other cool- and warmwater fish species.

Genetic status.—Genetic status determinations were based on genetic testing or likely sympatry with potentially hybridizing species, primarily introduced Coastal Rainbow Trout. Hybridizing fish could also include subspecies of Cutthroat Trout that have been introduced into habitats outside of their historic ranges. Streams occupied by Redband Trout were classified by hybridization status based on genetic testing, coexistence with potentially hybridizing species, or best professional judgment. Genetic information was available for approximately 450 sites. Genetic status was assigned to each existing population by biologists at workshops and entered for each stream segment and lake. In many cases, genetic sampling was not random because it occurred in streams thought to contain Redband Trout or with fish that phenotypically appeared to be Redband Trout. Consequently, the available genetic information did not represent a random sample from the populations throughout the entire distribution of Redband Trout.

Streams that were genetically tested and determined to support populations with less than 1% introgression were considered "unaltered." Streams that were determined to support populations with 1% or greater introgression were considered introgressed. Streams were deemed to contain a "mixed stock" when genetic testing revealed that a portion of the stock consisted of nonhybridized individuals that occurred in sympatry with individuals with varying levels of introgression, particularly in larger streams and rivers. When genetic data were not available, we used stocking records and the occurrence of potentially hybridizing species with Redband Trout to classify the likelihood of introgression (Shepard et al. 2005). Redband Trout were classified as "suspected unaltered" in streams for which stocking records and field surveys indicated the absence of potentially hybridizing species, whereas they were classified as "potentially altered" if any information indicated that potentially hybridizing species had ever been present. The lengths of stream occupied by each genetic category were summarized and the spatial distributions were displayed.

Habitat quality.—To assess habitat quality within the estimated current distribution of Redband Trout, stream segments were given a quality rating based on a number of habitat characteristics: pool quality and quantity, substrate conditions (percent fines and substrate composition), mean summer water temperature, instream cover, riparian habitat conditions (shading), streamflow, and other important habitat features. Biologists classified each stream segment as being in excellent, good, fair, or poor condition. Three physical habitat characteristics were then identified from a predetermined list of reference conditions that best described the evidence justifying the quality determinations (Table 2; Supplement). Habitat quality was not rated for lake environments.

Abundance.—We attempted to classify the densities of sexually mature Redband Trout (number of sexually mature fish per kilometer) for each currently occupied stream segment and lake (Schill et al. 2010). All fish ≥150 mm in small streams

TABLE 2. Quality reference conditions for interior Redband Trout habitat. Three attributes were selected to support the excellent/good and fair/poor classifications for each stream reach.

Attribute	Rating		Reference(s)
	Excellent/good	Fair/poor	
Fine sediment	<15% (desert) <7% (montane)	>25%	Meyer et al. 2010; Muhlfeld et al. 2001
Gravel/cobble/boulder	>50%	<50%	Meyer et al. 2010; Muhlfeld et al. 2001
Mean summer water temperature	10–16°C	<10°C, >16°C	Meyer et al. 2010; Raleigh et al. 1986
Pool or resting habitat (% of total area)	35–60%	<35%, >60%	Raleigh et al. 1986; Overton et al. 1995; Muhlfeld et al. 2001
Midday shade	>25%	<25%	Raleigh et al. 1986
Bank stability	>90%	<75%	Overton et al. 1995
Channel gradient	2–5%	>5%	Meyer et al. 2010; Muhlfeld et al. 2001

(≤4th order) and ≥250 mm in large streams (>4th order) were considered sexually mature. Redband Trout densities were classified as 0–35, 36–100, 101–250, 251–625, 626–1,250, and >1,250 fish/km as well as unknown.

Conservation populations.—Redband Trout populations currently being managed with an emphasis on conservation were identified as "conservation populations" based on their genetic, life history, or unique ecological or phenotypic characteristics (Shepard et al. 2005). Individual stream segments (currently occupied streams or lakes) that support Redband Trout and met at least one of the above conservation criteria were designated as conservation populations, with the potential to be aggregated in an individual stream or as part of a larger conservation metapopulation (sensu Hanski and Gilpin 1991). Aggregation of streams and/or lakes depended on connectivity among segments, suggesting that genetic exchange among local populations was likely occurring in both the upstream and downstream directions throughout the entire metapopulation. Where there are barriers to fish migration between stream segments, fish managers subdivided these stream segments into discrete, isolated populations. The information about each designated conservation population was summarized according to the number of subpopulations and the amount of stream and lake habitats occupied. Managers did not identify conservation populations in portions of the middle Snake River basin, including the Burnt and Powder rivers (Oregon) and the Weiser River (Idaho), due to incomplete knowledge of these watersheds or lack of time.

For each conservation population, a specific determination was made as to the primary reason for that designation. Core conservation populations were those with the highest potential for being genetically unaltered. This category included populations that had been genetically tested and found to be unaltered as well as populations that had not been tested but that were located in streams or lakes in which potentially hybridizing fish had not been stocked and were not present. Other classifications included populations having a known or probable unique life history (e.g., lacustrine–adfluvial or lacustrine outlet spawning), populations exhibiting an ecological adaptation to extreme environmental conditions (e.g., temperature, alkalinity, pH, or sediment), and subpopulations or habitat segments that included both nonintrogressed and introgressed individuals in a single conservation unit.

Conservation population vulnerability index.—We developed a conservation population vulnerability index (CPVI) to assess the status and threats to persistence of the individual Redband Trout conservation populations. Risks were classified as biotic, demographic, or abiotic using nine factors known to influence population viability, habitat quality, and future resilience (Table 3). Relative importance weights were applied to the different factors, and the results were combined into composite scores (Figure 2). This approach provided a flexible structure with which to evaluate the relative vulnerability of populations at any spatial scale of interest.

Biotic risks included hybridization with nonnative species, the introduction of species without the potential for hybridization, and disease. Hybridization risk was assessed in terms of the co-occurrence of Redband Trout with any nonnative species or subspecies capable of crossing with them. This risk depended primarily on the distance between the location of interest and those of such nonnative species as well as on the existence of barriers that would preclude contact with the conservation population (Table 3; Table S.31 in the online supplement). Introduced fish species without the potential for hybridization with Redband Trout were enumerated and ranked based on the number of such species co-occurring with each conservation population (Table 3). The diseases of concern were ones that could have severe negative effects on population health, including (but not limited to) whirling disease, furunculosis, and infectious pancreatic necrosis. As with the risk of hybridization, the risk of disease depended primarily on the distance to sources of disease and the existence of barriers to transmission (Table 3; Table S.32).

Demographic risks were assessed using measures of population connectivity (the number of occupied streams), population extent (the length of occupied streams), and life history diversity (the number of life history forms present; Table S.28). Abiotic risks were assessed using measures of habitat quality, the number of land-use practices in the area of interest (Table S.30), and the proportion of protected land in each stream network occupied by each conservation population. Because habitat quality was measured at individual streams, the habitat score was calculated as the mean stream values (Table S.17) weighted by stream length. If all of the stream habitat values applicable to the conservation population were unknown, the mean values for all streams within the 4th-level were used as a proxy. To calculate the proportions of protected land, streams were assigned to one (or more) land stewardship classes: protected (wilderness), managed (federal and state), and private. The proportions of the streams flowing through each of the classes were then multiplied by weighting factors (protected = 1, managed = 0.5, and private = 0) and summed to determine the class membership of the streams. Both empirical evidence and professional judgment were used to rank these risks. For several indicators risk data were unavailable for portions of some habitats occupied by conservation populations: hybridization (data unavailable for 4.7%), disease (37%), habitat quality (18.9%), land use (5%), and the presence of nonnative species (15.9%). For these missing data, we used the mean estimates of the indicators within each 8-digit HUC.

RESULTS

Historically and Currently Occupied Habitats

We estimated that interior Redband Trout historically occupied 60,295 km of stream habitat and 152 lakes and that they

TABLE 3. Risks assigned to populations of resident Redband Trout within the western United States designated as conservation populations, by risk category.

Risk category	Degree of risk	Risk attribute	Conservation significance
		Biotic risks	
Hybridization	Low	Hybridizing species cannot interact with existing Redband Trout population because a complete passage barrier is in place or hybridizing fish are not present in the same or any adjacent drainages.	Hybridization and introgression with nonnative salmonids are among the leading factors in declines of native resident Redband Trout.
	Medium–low	Hybridizing species are in the same stream, a drainage farther than 10 km from Redband Trout population, or both, but not in same stream segment as Redband Trout or within 10 km where a barrier currently exists (though that barrier may be at risk of failure).	
	Medium–high	Hybridizing species are in the same stream or a drainage within 10 km of the Redband Trout population and no barrier exists, or both; however, hybridizing species are not yet found in the same stream segment as the Redband Trout population.	
	High	Hybridizing fish are sympatric with the Redband Trout population.	
Introduced species	Low	Threats minor (0 nonnative species)	Introduced species negatively impact native populations through predation, competition, hybridization, disease, and parasites.
	Medium–low	Nonnatives present in watershed, but the chance of spreading is low (1 nonnative species)	
	Medium–high	Nonnatives present in watershed, and the chance of spreading is moderate (2 nonnative species)	
	High	Nonnatives present in watershed, and the chance of spreading is high (>2 nonnative species)	
Disease	Low	Significant diseases and the pathogens that cause them have very limited opportunity to interact with an existing Redband Trout population. Significant diseases and pathogens are not known to exist in stream or watershed.	Nonnative pathogens and parasites can infect Redband Trout and reduce their populations.
	Medium–low	Significant diseases, pathogens, or both have been introduced, identified, or both in the stream, a drainage farther than 10 km from the Redband Trout population, or both but not in same stream segment as the Redband Trout or within 10 km where barriers exist (though the barriers may be at risk of failure).	
	Medium–high	Significant diseases, pathogens, or both have been introduced, identified, or both, in the same stream, a drainage within 10 km of the Redband Trout population, or both, and no barriers exist.	

TABLE 3. Continued.

Risk category	Degree of risk	Risk attribute	Conservation significance
	High	Significant disease, pathogens, or both and disease-carrying species are sympatric with Redband Trout in the same stream segment.	
Demographic risks			
Population connectivity	Low	Occupied habitat consists of numerous (>5) individual streams and potential subpopulations are strongly networked.	Hydrologic connectivity provides more available habitat and facilitates expression of multiple life histories and genetic exchange, which increases the likelihood of persistence.
	Medium–low	Occupied habitat consists of a few (4–5) streams and potential subpopulations are moderately networked.	
	Medium–high	Occupied habitat consists of 2–3 streams and potential subpopulations are weakly networked.	
	High	Population isolated to a single stream or segment of stream, usually due to a barrier.	
Population extent	Low	At least 75 km of connected habitats; good connectivity	Small populations are more susceptible to stochastic events, thereby increasing their vulnerability to extirpation.
	Medium–low	≥25 and <75 km of connected habitats	
	Medium–high	≥10 and <25 km of connected habitats	
	High	<10 km of connected habitats; poor connectivity	
Life history diversity	Low	All four life history forms (resident, fluvial, adfluvial, and lacustrine–adfluvial) present	Loss of life history forms, particularly migratory forms, increases the risk of extirpation and loss of genetic diversity.
	Medium–low	Three life history forms present	
	Medium–high	Two life history forms present	
	High	Only one life history present	
Abiotic risks			
Habitat quality	Low	Stream habitat has the majority of attributes reflecting optimal conditions	Habitat conditions are a primary determinant of population persistence (see Table 2 for details on habitat attributes).
	Medium–low	Stream habitat has a few attributes that are slightly less than ideal	
	Medium–high	Stream habitat has more attributes that are less than ideal	
	High	Most stream habitat attributes reflect inferior conditions	
Land use	Low	No land use	Increased land use (e.g., timber harvest, grazing, mining, dams, etc.) reduces habitat quality quantity.
	Medium–low	1–2 types of land use	

TABLE 3. Continued.

Risk category	Degree of risk	Risk attribute	Conservation significance
Land ownership	Medium–high	3–4 types of land use	
	High	>4 types of land use	
	Low	≥30% of watershed in protected status	Watersheds with higher proportions of protected lands support higher quality habitat than do other lands.
	Medium–low	≥15% and <30% protected	
	Medium–high	≥1% and < 15% protected	
	High	<1% protected	

currently occupy 25,417 km of stream habitat (~42% of their historical distribution) and 124 lakes/reservoirs within the western United States (Figure 1; Tables 4, 5). Of the currently occupied habitat, 238 km of streams (1% of the total) and 92 lakes (74%) occur outside of historically occupied habitat. The estimated historical ranges of stream habitat by state were 21,556 km in Idaho (36%), 19,839 km in Oregon (33%), 10,598 km in Washington (18%), 4,606 km in California (7%), 2,606 km in Nevada (4%), 1,067 km in Montana (2%), and 23 km in Canada (the stream habitat in Canada was included to maintain the continuity of a single stream). Redband Trout currently occupy 11,016 km of stream habitat in Oregon (43% of the current distribution), 8,928 km in Idaho (35%), 2,828 km in Washington (11%), 1,301 km in Nevada (5%), 788 km in Montana (3%), 534 km in California (2%), and 21 km in Canada. Of the 10 major river basins (4-digit HUC) occupied by Redband Trout, the Middle Snake River basin supports the majority of stream length (46%; Table 1). Many of the stream segments (44%) currently occupied by Redband Trout are relatively small (<4 m wide; Table 5). A

total of 286 historical barriers (primarily waterfalls and cascades) and 561 contemporary barriers (primarily culverts and dams) were identified within the current distribution of Redband Trout. Nearly all (>99%) of Redband Trout occupying streams are of aboriginal origin (i.e., not introduced by humans).

Bootstrapped estimates of the proportion of historical habitat currently occupied by Redband Trout suggest generally low bias within and among the 4-digit HUCs (Figure 3). This conclusion is supported by the fact that mean values (and their associated confidence intervals) rapidly converged to the observed ratio of currently to historically occupied stream habitat within each HUC. For example, only 3 of the 10 geographic units (Kootenai–Pend Oreille–Spokane, Lower Snake, and North Lahontan) did not converge to the observed ratio until 40% or more of the data were included in the subsample.

Fish Stocking and the Presence of Nonnative Fish Species

Fish stocking was reported in 45% of the streams currently occupied by Redband Trout and nearly all (98%) of the occupied lakes. Coastal Rainbow Trout were the most commonly stocked species, followed by Cutthroat Trout, Brook Trout, and Brown Trout. Moreover, approximately 53% of currently occupied stream segments were reported to have at least one nonnative fish species present, 33% were reported to have no nonnative species, and 14% were classified as unknown. Of the currently occupied lakes, only 2% did not have any nonnative species present, whereas 23% reportedly contained nonnative fish; 75% were unknown. The nonnative fish coexisting with Redband Trout were primarily Rainbow Trout, Cutthroat Trout, Brook Trout, Brown Trout, and Smallmouth Bass *Micropterus dolomieu*.

Genetic Status

As of 2012, genetic data were available for approximately 450 sites; these data were used to infer genetic status in 4,473 km (18%) of occupied streams (Figure 1; Table 4). Genetic sampling produced no evidence of introgression in samples from 1,930 km of stream length (8% of currently
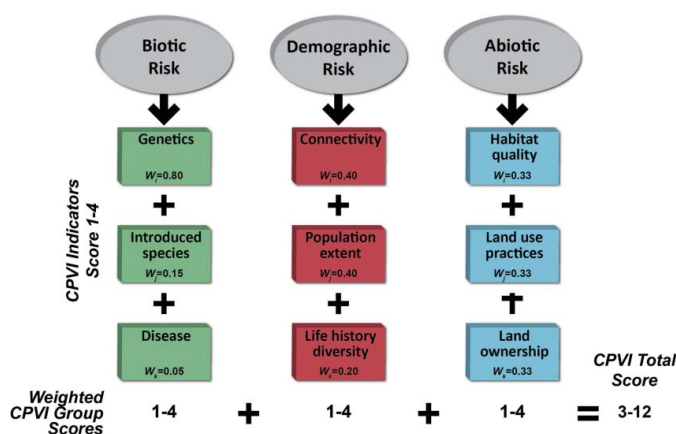

FIGURE 2. Schematic of the conservation population viability index (CPVI) used to assess the risks to Redband Trout conservation populations. The CPVI uses nine variables, which are divided into three general categories (biotic, demographic, and abiotic risks; see Table 3 for details). Each indicator is scored from 1 (very good) to 4 (poor), for a total of 12 possible points. [Color figure available online.]

TABLE 4. Genetic classes used for assessing the hybridization status of interior Redband Trout and their relative occurrence in the western United States as of 2012.

Genetic class	Stream		Lake	
	Km	% Occupied	Hectares	% Occupied
Tested; unaltered	1,930	8	35,030	19
Tested; 1–10% introgressed	1,303	5	6,765	4
Tested; 11–20% introgressed	469	2	393	<1
Tested; >20% introgressed	637	3	1,621	<1
Suspected unaltered	9,765	38	43,691	24
Potentially altered	11,179	44	60,376	33
Mixed stock (altered and unaltered)	134	1	36,628	20
Totals	25,417	100	184,504	100

occupied streams). Redband Trout were suspected to be genetically unaltered (but not tested) in approximately 9,800 km of streams and were likely part of a mixed-stock population in another 134 km. Thus, a maximum of 11,695 km (46%) of currently occupied stream habitat supports genetically unaltered Redband Trout, and the maximum proportion of the

historical range still supporting genetically unaltered Redband Trout is only 19%. Most of the stream length occupied by Redband Trout with no evidence of introgression occurred in the Middle Snake (907 km; 47%) and Kootenai–Pend Oreille–Spokane (576 km; 30%) basins. In contrast, no genetically pure (tested) populations were identified in the Lower Snake
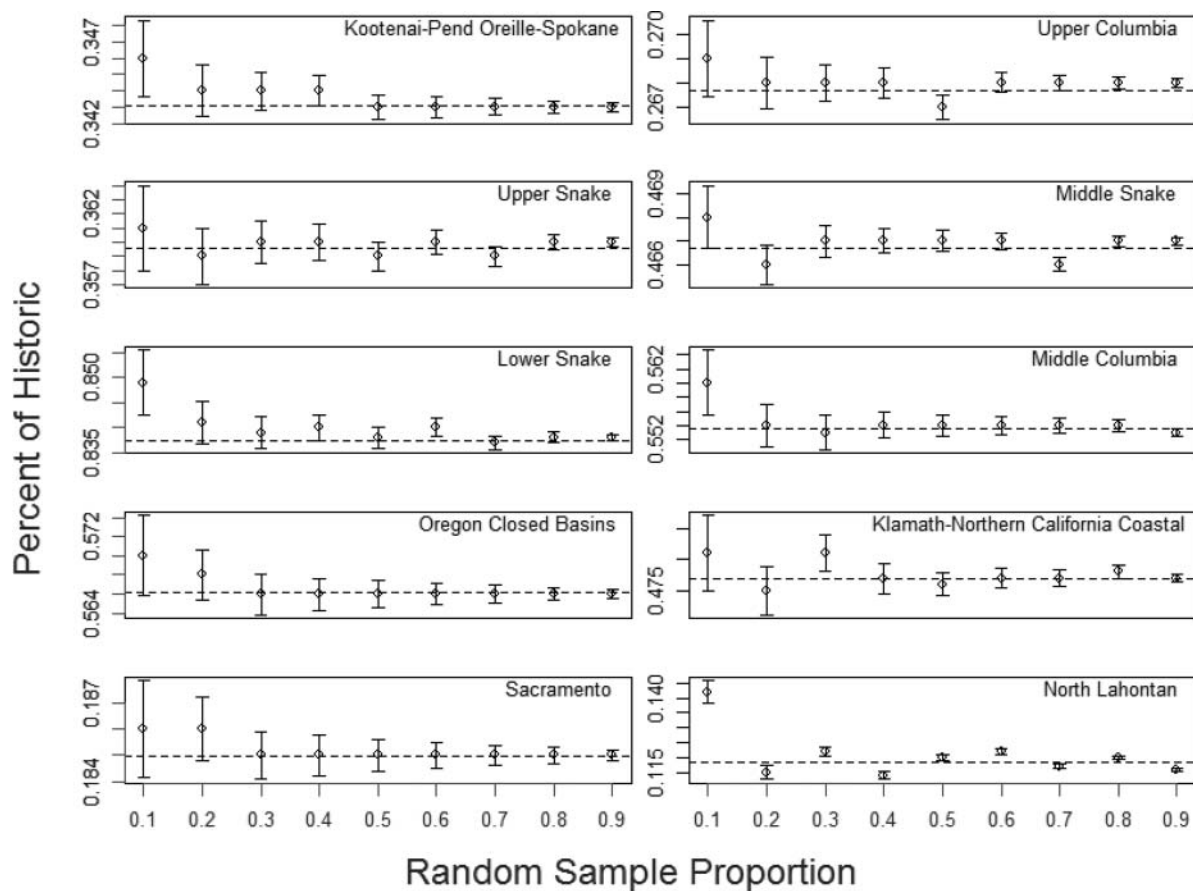

FIGURE 3. Bootstrapped estimates (1,000 iterations without replacement) of the proportions of historical habitat currently occupied by Redband Trout in major river basins (i.e., 4-digit HUCs). The dotted lines represent the total proportions (100% of the data) of currently occupied historical habitat.

TABLE 5.   Distribution of streams and rivers currently occupied by interior Redband Trout in the western United States, by estimated stream width.

Stream length	Stream width (m)							
	<2	2–3	4–6	7–10	11–15	>15	Unknown	Total
Kilometers	3,986	7,081	5,390	2,668	1,905	1,784	2,603	25,417
Percent	15.7	27.9	21.2	10.5	7.5	7.0	10.2	100

River and Lahontan basins and such populations were identified in only 9 and 10 km of stream habitat in the Sacramento and Klamath–northern California coastal basins, respectively. Additionally, genetic samples from approximately 35,000 ha (19%) of occupied lake habitats were judged to be genetically unaltered, and Redband Trout were suspected to be unaltered (but not tested) in an additional 43,691 ha (24%) of lake habitats. Lakes for which genetic testing found no evidence of introgression in Redband Trout that were coexisting with altered Redband Trout accounted for over 36,600 ha (20%) of lake habitats.

Land Ownership and Habitat Quality

Of the over 25,000 km of stream length currently occupied by Redband Trout, 8% was in protected areas (i.e., designated wilderness areas, roadless areas, or national parks), 45% was located within lands managed by government agencies, and 47% was in private lands (Figure 4).

Thirty-two percent of the stream habitat currently occupied by Redband Trout was rated as being in either excellent (5%) or good condition (27%), 34% was rated as being in fair condition, and 18% was rated as being in poor condition; no habitat quality rating was done for 16% of the occupied lotic habitats. The three most common habitat characteristics that led to the good-to-excellent quality ratings were (1) mean summer water temperatures within the optimum range of 10–16°C, (2) pool habitats comprising 35–60% of the total stream habitat area, and (3) adequate streamflow. The most common habitat characteristics that resulted in fair-to-poor quality ratings were (1) mean summer water temperatures exceeding 16°C, (2) fine sediment composition greater than 25%, and (3) lack of stream shading.

Abundance

No information was available for assessing Redband Trout density for 40% (10,081 km) of currently occupied streams. In stream segments for which estimates were available (Figure 5), fish densities were low (0–100 fish/km) in 48% (12,037 km) of currently occupied streams. Moderate fish densities (101–625 fish/km) were reported for 2,690 km (10% of currently occupied streams), and only 609 km (<3% of currently occupied streams) were classified as supporting high densities (>626 fish/km). Abundance levels exceeded 2,500

individuals in 39% (72,460 ha) of currently occupied lakes. No estimate of Redband Trout abundance was made for 107,488 ha (58%) of occupied lake habitat.

Conservation Populations

A total of 210 Redband Trout populations occupying 15,252 km of stream habitat (~60% of the current distribution) and 95,158 ha of lake habitats (~52%) are being managed as conservation populations. Conservation populations were widely distributed across the historical range of Redband Trout in the western United States, occurring in 56 of the 69
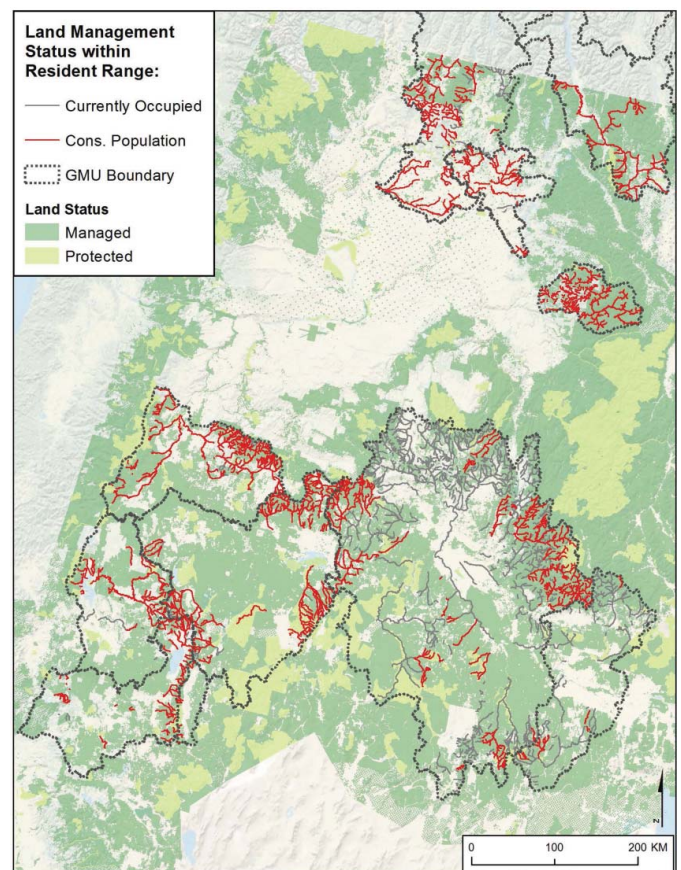

FIGURE 4. Map showing the current distribution of Redband Trout on managed (by local, state, and federal management agencies) and protected lands (e.g., those designated as wilderness areas, roadless areas, and national parks) within each geographical management unit (GMU). [Color figure available online.]
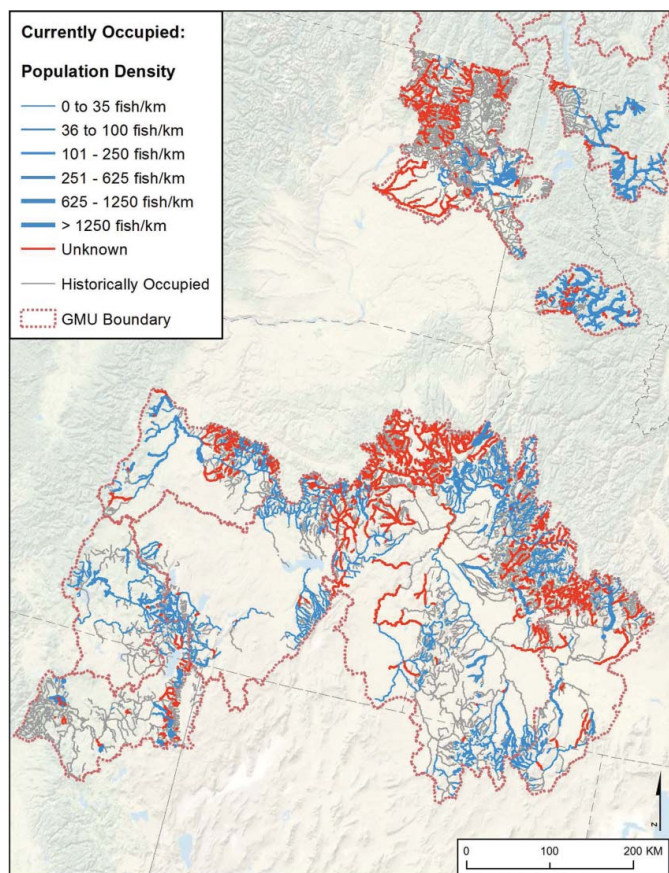
FIGURE 5. Map showing the estimated abundance of sexually mature Redband Trout (number of sexually mature fish per kilometer) throughout their range within the western United States. No information was available for projecting density for 40% (10,081 km) of currently occupied streams (red lines). [Color figure available online.]

historically occupied river basins (Figure 4). Conservation populations are widely distributed throughout the current range of Redband Trout, occurring in 81% of the watersheds analyzed, 60% of the streams, and 52% of the lakes. Individual conservation populations occupied from 0.2 to 1,279 km of lotic habitats (median = 18.9 km); however, the distribution of stream lengths occupied by conservation populations was skewed, with most populations occupying less than 20 km (N = 113; 54%). Most (60%) of the designated conservation populations were classified as weakly to strongly connected metapopulations that occupied much more stream length (14,112 km; 93%) than isolated populations (1,141 km; 7%; Table 6). One conservation population occupied only lake habitat and was not included in the CPVI assessment. Thirty-four conservation populations, occupying 6,754 km of stream length (44% of occupied stream length), were at high risk of hybridization, but the risk of hybridization was low for 75 populations occupying 2,519 km of stream length (17%). Low risks stemmed from the fact that populations were isolated upstream of fish passage barriers or hybridizing species were

not present in the same or adjacent drainages. Of the over 15,000 km of stream length occupied by conservation populations, 9% was in protected areas, 46% was within lands managed by government agencies, and 45% was on private land.

Of the 210 Redband Trout conservation populations, 49 (23%) were identified as core conservation populations (Table 7). The other conservation populations included 48 (23%) that were included based on their unique life histories, 33 (16%) that were included based on mixed genetic makeup, 24 (11%) with unique environmental adaptations, and 1 (located in the upper Pit River drainage) that has unique coloration and spotting similar to that of Cutthroat Trout. Fifty-five populations (26%) were placed in the "other" category.

The CPVI assessment suggested a broad range of risk for the persistence of Redband Trout populations. The overall mean CPVI (weighted by stream length) was 7.45 (Table 8; minimum possible score = 3, maximum = 12). The individual values ranged between 4.74 and 10.83. The areas of lowest risk for the loss of Redband Trout are in watersheds located in Oregon, Idaho, Washington, and northwestern Montana, where higher-quality habitat and relatively intact populations remain. In contrast, Redband Trout populations with relatively high risks of extinction are found in subwatersheds generally located at the fringes of their current distribution (including portions of northern Idaho and Washington) and along the southern margin of their historical range in northern California. The greatest risks to persistence for populations inhabiting the Kootenai–Pend Oreille–Spokane, Sacramento, and upper Columbia River basins were related to high demographic and abiotic risks, while biotic risks were greatest in the Lower Snake and portions of the Kootenai–Pend Oreille–Spokane River basins.

Habitat loss associated with land use and hybridization with nonnative salmonids were identified as the primary risks to designated conservation populations (Figure 6). Most of the stream length occupied by conservation populations (13,566 km; 89%) was classified as being at high risk owing to the negative effects of land use (primarily grazing, logging, roads, angling, and recreation), and most stream habitats (62%) were rated at medium-high to high risk because of degraded habitat quality conditions. Additionally, over 44% (6,754 km) of the occupied stream length was rated as being at high risk of genetic contamination because hybridizing species were sympatric with Redband Trout conservation populations. In contrast, most stream habitats were generally rated as being at low risk with respect to disease, population extent, and connectivity.

Conservation, restoration, and/or management actions have been taken, or are currently being taken, with respect to 165 of the 210 conservation populations (79%), and many conservation populations (61%) have had more than one conservation activity in at least part of their occupied lengths (Table 9). Habitat restoration activities (e.g., channel restoration, culvert replacement, bank stabilization, riparian fencing, and riparian

TABLE 6.   Numbers of isolated interior Redband Trout conservation populations and metapopulations (connected groups of subpopulations) in major river basins and numbers of river kilometers occupied.

River basin	Isolates		Metapopulations		Total		
	Number	Km	Number	Km	Number	Km	%
Kootenai–Pend Oreille–Spokane	17	152	22	1,587	39	1,739	11.4
Upper Columbia	17	128	16	1,605	33	1,733	10.9
Upper Snake	1	19	4	163	5	183	1.2
Middle Snake	10	277	29	3,545	39	3,822	25.1
Lower Snake	0	0	1	1,279	1	1,279	8.4
Middle Columbia	3	60	11	2,164	14	2,224	14.6
Oregon Closed Basins	16	282	12	2,187	28	2,469	16.2
Klamath–northern California coast	3	84	7	856	10	940	6.2
Sacramento	17	138	18	669	35	807	5.3
North Lahontan	0	0	5	57	5	57	0.4
Total	84	1,141	125	14,112	209	15,252	
Percent	40	7	60	93			

restoration) have been implemented for 107 of the conservation populations. Angling restrictions that are more stringent than those for general angling (e.g., catch and release) have been implemented for 31% of the conservation populations. Projects to remove nonnative species by physical or chemical means have been undertaken for about 5% of the conservation populations.

DISCUSSION

Distribution

Our analysis differed in several ways from previous distribution and status assessments of interior Redband Trout (Thurow et al. 1997, 2007). First, previous estimates of occupancy were based on watershed area, and Redband Trout were considered present in the entire subwatershed if they occurred anywhere in it. In contrast, we delineated potential historical and current distributions at a much finer reach or site scale (i.e., 1:24,000) based on updated hydrography (NHD) and advanced mapping tools (i.e., ArcGIS). Thus, our analysis likely yielded more accurate and precise estimates of historical and contemporary distributions and status. Second, although previous status assessments only included Redband Trout populations within the interior Columbia River basin and portions of the Klamath River and Great basins, we expanded the geographic domain of our assessment to include the historical range of the subspecies in the western United States, including areas in northern California and Nevada. Third, we incorporated a significant amount of new information that has emerged over the 16 years since the last Redband Trout distribution and status synthesis was completed (Thurow et al. 2007). Finally, we employed a standardized data management and analysis protocol (i.e., ICP) that has been applied to several other species of inland trout in the western United States (May et al. 2003; May and Albeke 2005; Shepard et al. 2005), which improves the documentation, consistency, and continuity for this and future assessments.

Although interior Redband Trout appear to be widely distributed in the western United States, we estimated a decline

TABLE 7.   Numbers of isolated interior Redband Trout conservation populations and metapopulations in major river basins and numbers of river kilometers occupied, by rationale for designation.

Rationale for designation	Isolates		Metapopulations		Total	
	Number	Km	Number	Km	Number	Km
Core conservation population	26	362	23	1,324	49	1,686
Ecological adaptation	13	259	12	1,773	25	2,032
Unique life history	15	158	33	4,135	48	4,292
Mixed genetic makeup	10	143	23	4,684	33	4,827
Other	20	220	34	2,196	54	2,415
Total	84	1,141	125	14,111	209	15,252

TABLE 8. Results of the conservation population vulnerability index (CPVI) assessment for interior Redband Trout in the United States, summarized by river basin. Primary risk components (biotic, demographic, and abiotic) were used to calculate values for each major river basin, disaggregated by state. Lower values indicate lower risk, higher values higher risk (see Table 3 for scoring details).

State/country	River basin	Stream km	Mean (SD)			
			CPVI	Biotic risk	Demographic risk	Abiotic risk
California	North Lahontan	57.3	7.33 (0.5)	2.22 (0.1)	2.76 (0.6)	2.35 (0)
	Oregon Closed Basins	5.3	6.13 (0)	1.0 (0)	2.8 (0)	2.33 (0)
	Sacramento	450.3	8.27 (0.8)	2.27 (0.7)	3.21 (0.7)	2.79 (0.4)
Canada	Kootenai–Pend Oreille–Spokane	21.6	8.01 (0)	3.86 (0)	1.2 (0)	2.96 (0)
Idaho	Kootenai–Pend Oreille–Spokane	262.4	8.38 (1.5)	2.52 (1.1)	2.96 (0.9)	2.9 (0.8)
	Lower Snake	1,279.0	7.26 (0)	3.71 (0)	1.2 (0)	2.35 (0)
	Middle Snake	2,437.6	7.14 (0.9)	2.14 (1.1)	2.7 (0.8)	2.3 (0.4)
	Upper Snake	62.6	7.73 (1.5)	2.51 (0.4)	2.85 (1.0)	2.37 (0.2)
Montana	Kootenai–Pend Oreille–Spokane	771.0	7.24 (1.2)	2.43 (1.3)	2.31 (1.2)	2.5 (0.5)
Nevada	Middle Snake	275.4	6.2 (0.5)	1.63 (0.4)	2.33 (0.9)	2.23 (0.2)
	Oregon Closed Basins	3.3	6.13 (0)	1.0 (0)	2.8 (0)	2.33 (0)
	Upper Snake	120.2	5.8 (0.4)	1.88 (0.1)	1.8 (0.6)	2.12 (0.1)
Oregon	Klamath–northern California	940.0	6.37 (1.3)	1.37 (0.4)	2.1 (0.9)	2.9 (0.3)
	Middle Columbia	2,223.6	7.59 (0.9)	2.83 (1.1)	2.14 (1.0)	2.63 (0.4)
	Middle Snake	1,109.3	7.49 (0.9)	2.53 (0.5)	2.17 (0.9)	2.79 (0.2)
	Oregon Closed Basins	2,460.0	7.43 (0.8)	1.82 (0.8)	2.95 (1.0)	2.66 (0.3)
	Sacramento	356.9	8.2 (0.9)	2.18 (0.1)	3.13 (1.1)	2.88 (0.3)
Washington	Kootenai–Pend Oreille–Spokane	759.8	8.85 (1.0)	2.6 (1.0)	3.18 (0.9)	3.07 (0.4)
	Upper Columbia	1,656.8	7.72 (0.9)	1.8 (0.8)	3.22 (0.9)	2.69 (0.6)

of 58% in historically occupied stream habitats. Introductions of nonnative species, habitat degradation, and habitat fragmentation were identified as the primary factors influencing the current distribution and status of interior Redband Trout, a finding that is consistent with previous status and distribution assessments for this subspecies. For example, Thurow et al. (2007) estimated that allopatric Redband Trout occupied 40% of their potential historical range in portions of the Columbia
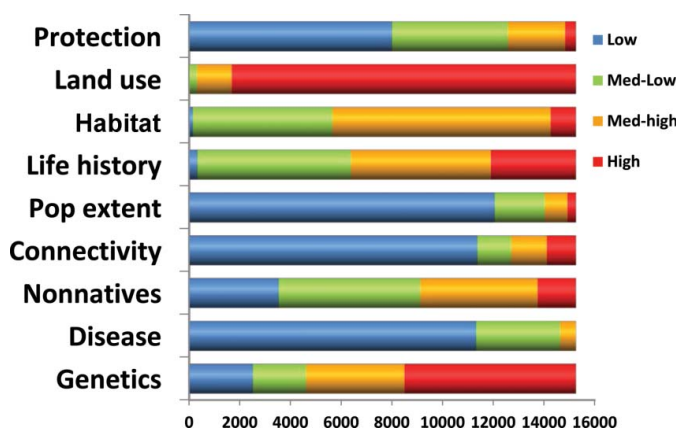

FIGURE 6. Relative extinction risks of Redband Trout populations by stream length (km) for the nine CPVI factors (see Table 3 for details). [Color figure available online.]

River basin and portions of the Klamath River and Great Basins using watershed areas, a finding similar to ours based on stream length (42%). Declines were more pronounced near the southern (California, Nevada, and southeastern Oregon) and northern (Washington) areas at the fringes of the historical range of Redband Trout in the United States.

Substantial reductions in the historical range of occupied habitats have also been reported for several other inland trout native to the western United States. For example, Gresswell (2011) estimated that Yellowstone Cutthroat Trout currently occupy 42% of their historical distribution, and May and Albeke (2005) reported a 65% decline for Bonneville Cutthroat Trout *O. clarkii utah*. Shepard et al. (2005) estimated that the historical distribution of Westslope Cutthroat Trout has declined 40%. In an extreme case, Hirsch et al. (2006) estimated that the Colorado River Cutthroat Trout *O. clarkii pleuriticus* only occupies 13% of its historical range.

Genetic Status

Nearly half of currently occupied stream length was assumed to support core (<1% introgressed) Redband Trout populations. However, genetic data were available for only 18% of currently occupied streams and 23% of lakes. Because of this and the relatively high potential for hybridization with nonnative salmonids (particularly hatchery-origin Rainbow

TABLE 9. Numbers and percentages (based on the 210 populations that were evaluated) of Redband Trout conservation populations in the western United States that have been subject to various types of conservation, restoration, and management actions as of 2012.

Conservation action	Number	Percentage
Angling regulations	66	31.4
Bank stabilization	52	24.8
Barrier construction	6	2.9
Barrier removal	38	18.1
Channel restoration	57	27.1
Chemical removal of competing–hybridizing species	7	3.3
Culvert replacement	46	21.9
Diversion modification	28	13.3
Fish ladder installation	14	6.7
Fish screen installation	24	11.4
Grade control	14	6.7
Instream cover habitat	29	13.8
Irrigation efficiency	11	5.2
Land-use mitigation direction and requirements	87	41.4
Physical removal of competing–hybridizing species	4	1.9
Pool development	30	14.3
Population restoration or expansion	2	1.0
Population supplementation	1	0.5
Public outreach (interpretive site)	19	9.0
Refounding of pure population	3	1.4
Riparian fencing	65	31.0
Riparian restoration	71	33.8
Spawning habitat enhancement	12	5.7
Water lease–flow enhancement	16	7.6
Watershed under protective management	46	21.9
Woody debris addition	44	21.0

Trout), the actual genetic status of interior Redband Trout is probably less certain than these data suggest.

The majority of stream length occupied by core populations was located in the Middle Snake (47%) and Kootenai–Pend Oreille–Spokane (30%) River basins, suggesting that these areas are a priority for the conservation of Redband Trout populations. As of 2012, core populations had not been documented in the Lower Snake River or Lahontan basins. These findings, however, are likely correlated with the amount of stream habitat for which genetic testing has been conducted. For example, as of 2012 no genetic data were available for Redband Trout populations in the Lower Snake River basin.

Fish managers have identified several habitat characteristics that are important to Redband Trout across a variety of habitats, ranging from desert streams in arid landscapes to forested montane streams. Mean summer water temperature, streamflow, habitat complexity, substrate composition, and stream shading have all been identified as important factors in determining habitat quality. In desert streams, several studies have shown that stream-shading bank cover and stability, substrate composition, and habitat connectivity are important habitat features in the distribution and abundance of Redband Trout

(Zoellick 1999, 2004; Zoellick et al. 2005; Zoellick and Cade 2006; Meyer et al. 2010). Water temperature, which has direct effects on the physiology, behavior, and ecological interactions of Redband Trout (Cassinelli and Moffitt 2010; Feldhaus et al. 2010; Kammerer and Heppell 2013), has been identified as an important determinant of habitat quality across a wide range of environmental conditions, especially in hot, arid rangeland basins. In desert streams, the occurrence and biomass of Redband Trout have been strongly associated with shaded reaches of streams with less solar radiation, cooler stream temperatures, and abundant pools (Li et al. 1994; Zoellick 1999, 2004; Tate et al. 2007; Meyer et al. 2010). In montane streams, the distribution and abundance of Redband Trout has been positively related to the abundance of deep pools with complex cover and negatively related to stream gradient (Muhlfeld 2002; Muhlfeld et al. 2001a, 2001b; Meyer et al. 2010).

Land Ownership and Habitat Quality

Most of the stream and lake habitats currently occupied by Redband Trout occur on private lands or lands managed by

governmental agencies. The relatively small amount of habitat located in protected areas (8% of the total occupied) will likely serve as refugia for population strongholds and future restoration and recovery efforts. The long-term persistence of Redband Trout will largely depend on local, state, federal, tribal, and nongovernmental agencies and private land owners working collectively to develop and implement conservation and restoration programs across large landscapes.

Threats

Habitat degradation, habitat fragmentation, nonnative species introductions, and climate change were identified as primary threats to existing populations of Redband Trout. Land and water use practices have degraded aquatic habitats and severed the connections between aquatic habitats that are necessary for the long-term persistence of Redband Trout. Extensive translocations of nonnative species have displaced and caused extensive hybridization with native Redband Trout populations in many watersheds. Compounding the effects of these stressors is climate change, which is expected to increase water temperatures, modify hydrologic regimes, and increase disturbance events throughout the western United States (Wenger et al. 2011), likely putting many populations at further risk of decline and extirpation (Williams et al. 2009; Haak et al. 2010a).

Our data suggest that the introduction and expansion of nonnative species have negatively influenced the status and distribution of interior Redband Trout. Extensive stocking of nonnative fishes for management purposes has resulted in the coexistence of nonnative fishes with native Redband Trout in over 50% of streams and nearly all lakes and reservoirs. Invasions and translocations of exotic species have led to major changes in native biological communities (Vitousek et al. 1997; Rahel 2000) and have been a primary contributor to species extinctions in freshwater ecosystems (Miller et al. 1989; Rhymer and Simberloff 1996; Mooney and Cleland 2001) through competition, predation, hybridization, disease, and parasites (Krueger and May 1991; Mooney and Cleland 2001).

Introductions of nonnative salmonids (primarily hatchery Rainbow Trout) have resulted in extensive hybridization across the historical range of interior Redband Trout and pose an imminent threat to many remaining populations. We found that widespread introduction of nonnative Rainbow Trout throughout the historical range of Redband Trout has resulted in the expansion of hybridization and in many cases to the irreversible replacement of native populations with hybrid swarms. Hybridization between native trout and introduced salmonids is an increasing concern for conservation and legal assessments for many species, including many native trout species in the western United States (Allendorf et al. 2001, 2005). In trout, hybridization can reduce fitness through outbreeding depression due to the disruption of coadapted gene complexes and the erosion of local adaptations (Rhymer and

Simberloff 1996; Muhlfeld et al. 2009) and cause genomic extinction (Allendorf et al. 2001). Furthermore, habitat modification (Allendorf et al. 2001) and climate warming often exacerbate the effects of hybridization (Muhlfeld et al. 2014). Therefore, hybridization is likely to become more serious as it interacts with increasing anthropogenic land use, global climate change, and the introduction of nonnative species, suggesting that further declines in native genetic diversity are likely for Redband Trout.

Hybridization resulting from translocations of hatchery-origin Rainbow Trout and nonnative Cutthroat Trout has been reported in several other studies throughout the range of Redband Trout (Small et al. 2007; Dambacher et al. 2009; Simmons et al. 2010; Kozfkay et al. 2011; Neville and Dunham 2011). In Idaho streams, Neville and Dunham (2011) found that several native Redband Trout populations have been almost completely replaced with hatchery Rainbow Trout and hybrid swarms, while others retained high genetic integrity and could be prioritized for conservation. In the upper Snake River basin in Idaho, Kozfkay et al. (2011) and Meyer et al. (2014) found that the hybridization of Redband Trout with hatchery Rainbow Trout was more prevalent in streams where stocking had occurred but that Redband Trout were more likely to be genetically unaltered in streams without such stocking. In contrast, high levels of hybridization with nonnative Cutthroat Trout were detected in only a few streams. Knudsen et al. (2002) found that genetically unaltered Redband Trout populations only persist above natural barriers (i.e., waterfalls) in the upper Kootenai River drainage in Montana and Idaho. Hybridization with nonnative Rainbow Trout is a pervasive threat to all inland extant subspecies of Cutthroat Trout in western North America and has contributed to the extinction of two Cutthroat Trout subspecies (Behnke 1992).

By virtue of their effects on habitat, agricultural practices, grazing, water diversion, dams, mining, timber harvest, recreation, and road construction have been identified as leading threats to interior Redband Trout. These anthropogenic activities have been shown to negatively impact trout habitats and populations in lotic environments throughout the United States by imposing barriers to migration and causing reductions in streamflow, increased sedimentation, groundwater depletion, increased water temperature, and the simplification of aquatic habitats (Meehan 1991). Most of these activities have been reported to occur on nonfederal lands at lower elevations (Meehan 1991) but they are common across the current range of Redband Trout except in protected areas. Low-elevation streams have suffered from extensive agricultural and residential development. The construction and operation of dams, irrigation diversions, and other barriers to migration have isolated populations and eliminated habitats that were previously available to migratory populations. The loss of migratory forms and gene flow among populations reduces the long-term viability of metapopulations (Rieman and McIntyre 1995). Isolation of

Redband Trout populations in headwater streams increases the risk of extirpation due to demographic and environmental stochasticity and the loss of genetic diversity.

Habitat modifications caused by various land and water use practices have impacted interior Redband Trout populations and habitats throughout their current range (Williams et al. 1989). In a study of the cumulative effects of riparian disturbance in high-desert streams in Oregon, Li et al. (1994) found that watersheds with greater riparian canopy, lower daily maximum temperatures, and perennial flow had higher densities of Rainbow Trout. Land development activities such as road construction, logging, and grazing can alter substrate composition and reduce the frequency and area of pools, which are critical to Redband Trout in the headwaters of the Columbia River basin in Montana and Idaho (Muhlfeld et al. 2001a, 2001b; Muhlfeld 2002). Many desert populations of interior Redband Trout are threatened by the degradation of stream and riparian habitat and the increased water temperatures resulting from grazing and agricultural practices (Zoellick 2004; Zoellick et al. 2005; Zoellick and Cade 2006; Johnson and Fite 2007; Bayley and Li 2008). Artificial barriers have isolated many Redband Trout populations and eliminated habitats that were previously available to migratory populations (Thurow et al. 2007; Holecek et al. 2012; Holecek and Scarnecchia 2013).

Although we did not assess the vulnerability of Redband Trout to future climate change, several key indicators of population risk identified in the CPVI assessment may be important in assessing the resiliency of populations and their capacity to adapt to environmental change associated with climate warming. Salmonids such as Redband Trout are especially vulnerable to the effects of climate change in freshwater systems because they require cold, connected, and high-quality habitats free of nonnative salmonids; such habitats are easily fragmented by changes in thermal and hydrologic regimes and biological invasions. A number of bioclimatic models have recently been developed for native trout in the western United States, all of which forecast substantial reductions in suitable habitat during the 21st century (Keleher and Rahel 1996; Wenger et al. 2011; Isaak et al. 2012). These models all show that as water temperatures continue to rise and exceed the physiological thresholds of native trout populations, habitats will likely become increasingly fragmented and fish will retreat into cooler headwater streams. For example, using an upper temperature threshold of 22°C as a constraint for coldwater trout and char, Keleher and Rahel (1996) predicted that an increase of 5°C in mean air temperature would reduce the amount of thermally suitable salmonid habitat by 70% across the Rocky Mountain region.

In the western United States, climatic trends and regional climate models suggest that not only will stream habitats become warmer, they will also become more variable in terms of their thermal and hydrologic regimes; more susceptible to stochastic disturbances such as flooding, wildfire, and drought;

and more prone to invasion by nonnative species. Wenger et al. (2011) forecasted the climate warming effects of higher temperatures, altered flow regimes, and interactions with nonnative species on four interacting species of trout and predicted about a 50% decline in total suitable trout habitat across the interior western United States by 2080. Muhlfeld et al. (2014) found that climate-induced increases in stream temperature and periods of reduced spring precipitation accelerated hybridization between native Westslope Cutthroat Trout and nonnative Rainbow Trout. Thus, impending climate change could directly or indirectly lead to greater habitat and population fragmentation and hybridization, further accelerating the decline of Redband Trout populations across the western United States. However, we expect that such changes will not be uniform across the range of Redband Trout given their broad geographic distribution and adaptations to a wide variety of environmental conditions. Research is needed to better assess the vulnerability of Redband Trout populations to future climate warming (see below).

Conservation Populations

Fish managers have designated conservation populations based on genetic integrity, unique life history traits, and ecological adaptations. Conservation populations consist of genetically pure, introgressed, and genetically untested populations. Managers have emphasized the conservation of genetic integrity by designating 49 core populations (23%), which encompass about half of the stream length occupied by conservation populations. Isolated populations account for 40% of the designated conservation populations, but these populations occupy only 7% of the total stream length occupied by conservation populations. These populations are generally at low risk of introgression because they are isolated from potentially hybridizing species by natural or artificial barriers. Conversely, we found that about half of the stream length occupied by conservation populations supports populations with some level of genetic introgression (>1%). In these cases, the conservation populations are likely part of a larger, interconnected metapopulation that was designated to conserve migratory life history characteristics (e.g., migratory forms) and unique ecological adaptations (e.g., thermal tolerances). Conservation populations that are part of weakly to strongly connected metapopulations occupy much more stream length (93%) than conservation populations that are isolated (7%). Genetic testing was only conducted in 22% of the stream length occupied by conservation populations.

Active conservation and restoration are occurring for many populations of interior Redband Trout. Watershed and stream habitat restoration activities (e.g., channel restoration, culvert replacement, bank stabilization, riparian fencing, and riparian restoration) have been implemented for a majority of conservation populations. The mitigation of harmful forms of land use through forest plans, regulations, permits, and agency

coordination has been identified as an important conservation action for many waters. Angling restrictions that are more stringent than general angling regulations have been implemented for over 30% of the conservation populations.

Surprisingly, projects to physically or chemically remove nonnative species have taken place for only seven Redband Trout conservation populations. Physical and chemical rehabilitation techniques have proven useful for eliminating or reducing the impacts of invasive species on many native trout species. We suspect that invasive species and genetic introgression will continue to spread unless nonnative and hybrid populations, especially those with large amounts of nonnative genetic admixture, are reduced or eliminated.

We found that fish barriers are being used to isolate Redband Trout populations from the threats of genetic introgression, competition with and predation by nonnative fish, and disease in only a few cases. Isolation by artificial barriers is often used as a conservation strategy for native trout in small headwater streams (Fausch et al. 2009). However, the isolation of Redband Trout populations in small headwater habitats may increase the risk of extinction due to demographic and genetic stochasticity (Franklin 1980; Peterson et al. 2008). Maintaining large areas of connected habitat is also an important conservation strategy that has been identified by managers, with the goal of allowing Redband Trout to express all life history traits and reducing stochastic environmental and demographic risks. However, this strategy will likely increase the risk of introgression, competition with and predation by nonnative fish, and disease for some connected populations. Thus, the difficult trade-offs in managing native Redband Trout by creating barriers to upstream movement and providing large connections of diverse habitats for life history expression will require difficult and context-specific decisions (Peterson et al. 2008). Suppression and/or eradication of source populations in headwater lakes will be necessary in cases where hybrid sources threaten downstream nonhybridized Redband Trout populations.

We developed the CPVI to integrate complex assemblages of ICP data into an easily digestible metric that managers can use to make informed decisions about the management of individual Redband Trout conservation populations. The CPVI was based on a similar index, the conservation success index (CSI; Williams et al. 2007), that included biotic, demographic, and abiotic risks based on nine factors known to influence population integrity, habitat integrity, and potential future security. A notable distinction between the CPVI and the CSI is in the weighting of the individual metrics used to calculate the indices. We chose to heavily weight the biotic risk score because hybridization with nonnative salmonids was the greatest threat to the persistence of Redband Trout in our assessment. However, our CPVI framework is flexible and allows managers to weight risks differently depending on the particular situation. The CPVI can be combined with additional data (such as climate scenarios and proposed land management modifications) as well as expert opinion to further inform management actions and prioritize the allocation of limited resources for Redband Trout conservation (Williams et al. 2009; Haak et al. 2010b).

Our CPVI assessment generally indicated that peripheral populations (those at the geographic edge of their range) are at higher risk than populations in the core of their range. Similarly, in analyzing the rangewide habitat loss of peripheral and core populations of five Cutthroat Trout subspecies in the western United States, Haak et al. (2010b) found that the more isolated, peripheral populations experienced greater losses of habitat. Peripheral populations have become increasingly valuable for the conservation of declining species because they often maximize within-species genetic and ecological diversity and retain their evolutionary legacy and genetic diversity, thereby allowing for possible future adaptation to extreme environmental pressures (Haak et al. 2010b), especially in the face of accelerating human impacts and climate change.

Limitations and Future Work

We acknowledge the limitations of the database and the inherent uncertainties of an assessment using expert opinion and anecdotal information. We tested our results for biases that may have been introduced by using expert opinion across management areas and the sensitivity of the occupancy data to the variation in reach lengths inherent within the NHD. Bootstrapped estimates of the proportion of historical habitat currently occupied by Redband Trout indicate generally low bias within and among geographic management units. We recommend that future estimates of occupancy follow a more rigorous spatial sampling design that incorporates estimates of detection probabilities, sampling error, and the reliability of presence/absence data across various geographic areas and stream environments, at least for some areas within the historical range of Redband Trout.

Based on biologists' assignment of genetic categories, we inferred that approximately 450 sites have had some level of genetic validation; however, data documenting the genetic testing protocols (genetic testing methodology, number of fish sampled, and number of diagnostic loci evaluated) and the exact sampling locations were not available to us during this assessment. Consequently, we could not fully evaluate the limitations of these genetic data. We strongly recommend that detailed genetic testing information be included in these types of assessments and suggest that more genetic testing is needed to confirm the genetic status of existing populations, especially conservation populations.

Knowing the sample sizes (numbers of fish and diagnostic loci) of genetic tests would allow one to test the statistical power of each genetic sampling event. Recently developed genomic techniques can identify and characterize thousands of species-diagnostic markers to precisely estimate population- and individual-level admixture so as to better understand the

genetic status of native trout populations (Sprowles et al. 2006; Blankenship et al. 2011; Hohenlohe et al. 2011, 2013; Amish et al. 2012). Such approaches are urgently needed for Redband Trout. Once genetic sampling and analyses are well documented, it will be possible to more precisely quantify their genetic status in relation to the level of genetic testing.

Comprehensive assessments of regional climate trends and population responses are needed to inform and predict the impacts of changes in climate across the current range of Redband Trout. Additional population monitoring data combined with high-resolution hydroclimatic data (e.g., stream temperature, streamflow, snowpack, precipitation, etc.) are needed to evaluate how climate warming will influence the distribution, abundance, phenology, and genetic diversity of Redband Trout. For example, recent advances in the geostatistical modeling of stream systems have greatly improved temperature prediction by using spatially explicit data to explain the variation across heterogeneous river networks (Peterson and Ver Hoef 2010). These types of fish population, habitat, and climate monitoring data and spatially explicit forecasting tools are needed to help direct conservation actions (e.g., stream restoration and habitat protection) at the local (i.e., stream reach) and watershed scales to improve population resiliency and adaptive capacity in the face of climate warming. Such data could be formally included in future updates of this assessment.

The conservation of Redband Trout will require protecting evolutionary processes, adaptive potential, and ecological variation within major evolutionary units. However, the taxonomic nomenclature and phylogenetic divisions currently remain unresolved among inland groups of Redband Trout. Phylogenetics offers a promising approach to resolve discrepancies because it combines processes influencing the geographic distributions of species with their genealogical lineages to identify evolutionarily significant groups (e.g., Currens et al. 2007). Specifically, this approach combines patterns of genetic variation with measures of adaptive significance and ecological uniqueness to maintain adaptive potential within species. Genetic variation can be assessed on different timescales, from current family pedigrees and population structure (determined from microsatellites or single-nucleotide polymorphisms) to phylogenetic variation (determined from mtDNA) over thousands to millions of years, thus reflecting both contemporary and evolutionary relationships. Ecological distinctness involves consideration of unique adaptive traits, such as life history, ecological requirements, morphology, and demographic characteristics. These types of ecological and genetic data are needed to identify, prioritize, and conserve major evolutionary units of Redband Trout to ensure preservation of the evolutionary legacy and adaptive potential of the species.

Our CPVI assessment integrates data on a number of variables from a variety of sources to help managers assess risk and prioritize conservation actions across the range of Redband Trout in the United States. Risk variables were classified with constructed scales based on simple interpretations (e.g., threats were classified as low, medium-low, medium-high, and high), which were then converted to numerical scores. However, ordinal numbers do not necessarily reflect how much one score is better than another, and the ultimate conservation prioritizations may be influenced by the choice of metrics (Game et al. 2013). We recommend that future CPVI assessments attempt to reduce these uncertainties by using empirical data to identify the most important variables influencing population persistence and by estimating the values of variables on natural scales wherever possible.

Conclusions

In this article, we provide baseline status and distribution information that can be used to assess ongoing and future conservation management programs and to prioritize and plan for the restoration and protection of interior Redband Trout across the western United States. We recommend maintaining the ICP assessment database (providing clear documentation for it and utilizing consistent protocols) and periodically updating these data to track changes in genetic status, the distribution and abundance of Redband Trout, nonnative species, diseases, anthropogenic impacts, habitat conditions, and the impacts of climate change over time. This type of database and standardized and systematic data collection efforts are needed to monitor the status of Redband Trout over time. We are concerned that the true genetic status of existing populations has not been well quantified and that genetic introgression may be more prevalent than documented here. Therefore, we recommend collecting additional genetic information to better quantify the hybridization status and geographic structuring of existing populations. Additionally, we suggest estimating the distributions and abundances of Redband Trout populations using a more rigorous spatial sampling design to reduce sampling uncertainties. Understanding and predicting the vulnerability of Redband Trout populations to future climate warming will be critical to managing and preserving this species in a warming world.

Conservation management strategies that protect genetically pure populations and eliminate or reduce nonnative species and hybridized populations will be necessary to maintain the genetic integrity and ecological diversity of Redband Trout. Maintaining natural connections and a diversity of high-quality habitats over a large spatial scale will be crucial to conserving the full expression of life history traits, genetic diversity, and the processes influencing the dispersal and persistence of Redband Trout populations. Protection of genetic reserves and replication of genetically pure populations may be necessary in cases in which populations are at high risk of extirpation and to enable the refounding Redband Trout in their historical habitats. Conservation strategies that provide larger population sizes and a broader mosaic of larger habitat

patches will be needed to maintain and restore the genetic and ecological diversity of Redband Trout.

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REFERENCES

Allendorf, F. W. 1975. Genetic variability in a species possessing extensive gene duplication: genetic interpretation of duplicate loci and examination of genetic variation in populations of Rainbow Trout. University of Washington, Seattle.

Allendorf, F. W., R. F. Leary, N. P. Hitt, K. L. Knudsen, M. C. Boyer, and P. Spruell. 2005. Cutthroat Trout hybridization and the U.S. Endangered Species Act: one species, two policies. Conservation Biology 19:1326–1328.

Allendorf, F. W., R. F. Leary, P. Spruell, and J. K. Wenburg. 2001. The problems with hybrids: setting conservation guidelines. Trends in Ecology and Evolution 16:613–622.

Amish, S. J., P. A. Hohenlohe, S. Painter, R. F. Leary, C. Muhlfeld, F. W. Allendorf, and G. Luikart. 2012. RAD sequencing yields a high success rate for Westslope Cutthroat and Rainbow trout species: diagnostic SNP assays. Molecular Ecology Resources 12:653–660.

Atkinson, S. D., and J. L. Bartholomew. 2010. Spatial, temporal, and host factors structure the *Ceratomyxa shasta* (Myxozoa) population in the Klamath River basin. Infection Genetics and Evolution 10:1019–1026.

Bayley, P. B., and H. W. Li. 2008. Stream fish responses to grazing exclosures. North American Journal of Fisheries Management 28:135–147.

Behnke, R. J. 1992. Native trout of western North America. American Fisheries Society, Monograph 6, Bethesda, Maryland.

Berg, W. J. 1987. Evolutionary genetics of Rainbow Trout, *Parasalmo gairdneri* (Richardson). University of California, Davis.

Blankenship, S. M., M. R. Campbell, J. E. Hess, M. A. Hess, T. W. Kassler, C. C. Kozfkay, A. P. Matala, S. R. Narum, M. M. Paquin, M. P. Small, J. J. Stephenson, K. I. Warheit, and P. Moran. 2011. Major lineages and metapopulations in Columbia River *Oncorhynchus mykiss* are structured by dynamic landscape features and environments. Transactions of the American Fisheries Society 140:665–684.

Buchanan, D. V., J. E. Sanders, J. L. Zinn, and J. L. Fryer. 1983. Relative susceptability of 4 strains of summer steelhead to infection by *Ceratoymyxa shasta*. Transactions of the American Fisheries Society 112:541–543.

Cassinelli, J. D., and C. M. Moffitt. 2010. Comparison of growth and stress in resident Redband Trout held in laboratory simulations of montane and desert summer temperature cycles. Transactions of the American Fisheries Society 139:339–352.

Currens, K. P. 1997. Evolution and risk in conservation of Pacific salmon. Oregon State University, Corvallis.

Currens, K. P., C. B. Schreck, and H. W. Li. 2007. Evolutionary diversity in Redband Trout. Pages 10–11 *in* R. K. Schroeder and J. D. Hall, editors. Redband Trout: resilience and challenge in a changing landscape. American Fisheries Society, Oregon Chapter, Corvallis.

Currens, K. P., C. B. Schreck, and H. W. Li. 2009. Evolutionary ecology of Redband Trout. Transactions of the American Fisheries Society 138:797–817.

Dambacher, J. M., K. K. Jones, and D. P. Larsen. 2009. Landscape-level sampling for status review of Great Basin Redband Trout. North American Journal of Fisheries Management 29:1091–1105.

Fausch, K. D., B. E. Rieman, J. B. Dunham, M. K. Young, and D. P. Peterson. 2009. Invasion versus isoloation: trade-offs in managing native salmonids with barriers to upstream movement. Conservation Biology 23:859–870.

Feldhaus, J. W., S. A. Heppell, H. Li, and M. G. Mesa. 2010. A physiological approach to quantifying thermal habitat quality for Redband Rainbow Trout (*Oncorhynchus mykiss gairdneri*) in the South Fork John Day River, Oregon. Environmental Biology of Fishes 87:277–290.

Franklin, I. R. 1980. Evolutionary changes in small populations. Pages 135–140, *in* M. E. Soule and B. A. Wilcox, editors. Conservation biology: an evolutionary–ecological perspective. Sinauer, Sunderland, Massachusetts.

Game, E. T., P. Kareiva, and H. P. Possingham. 2013. Six common mistakes in conservation priority setting. Conservation Biology 27:480–485.

Gamperl, A. K., K. J. Rodnick, H. A. Faust, E. C. Venn, M. T. Bennett, L. I. Crawshaw, E. R. Keeley, M. S. Powell, and H. W. Li. 2002. Metabolism, swimming performance, and tissue biochemistry of high desert Redband Trout (*Oncorhynchus mykiss* ssp.): evidence for phenotypic differences in physiological function. Physiological and Biochemical Zoology 75:413–431.

Gresswell, R. E. 2011. Biology, status, and management of the Yellowstone Cutthroat Trout. North American Journal of Fisheries Management 31:782–812.

Haak, A. L., J. E. Williams, D. Isaak, A. Todd, C. C. Muhlfeld, J. L. Kershner, R. E. Gresswell, S. W. Hostetler, and H. M. Neville. 2010a. The potential influence of climate change on the persistence of salmonids of the inland West. U.S. Geological Survey, Open-File Report 2010-1236, Reston, Virginia.

Haak, A. L., J. E. Williams, H. M. Neville, D. C. Dauwalter, and W. T. Colyer. 2010b. Conserving peripheral trout populations: the values and risks of life on the edge. Fisheries 35:530–549.

Hanski, I., and M. Gilpin. 1991. Metapopulation dynamics: brief history and conceptual domain. Biological Journal of the Linnean Society 42:3–16.

Hirsch, C. L., S. E. Albeke, and T. P. Nesler. 2006. Rangewide status of Colorado River Cutthroat Trout (*Oncorhynchus clarkii pleuriticus*): 2005. Wyoming Game and Fish Department, Cheyenne.

Hohenlohe, P. A., S. J. Amish, J. M. Catchen, F. W. Allendorf, and G. Luikart. 2011. Next-generation RAD sequencing identifies thousands of SNPs for assessing hybridization between Rainbow and Westslope Cutthroat trout. Molecular Ecology Resources 11:117–122.

Hohenlohe, P. A., M. D. Day, S. J. Amish, M. R. Miller, N. Kamps-Hughes, M. C. Boyer, C. C. Muhlfeld, F. W. Allendorf, E. A. Johnson, and G. Luikart. 2013. Genomic patterns of introgression in Rainbow and Westslope Cutthroat trout illuminated by overlapping paired-end RAD sequencing. Molecular Ecology 22:3002–3013.

Holecek, D. E., and D. L. Scarnecchia. 2013. Comparison of two life history strategies after impoundment of a historically anadromous stock of Columbia River Redband Trout. Transactions of the American Fisheries Society 142:1157–1166.

Holecek, D. E., D. L. Scarnecchia, and S. E. Miller. 2012. Smoltification in an impounded, adfluvial Redband Trout population upstream from an impassable dam: does it persist? Transactions of the American Fisheries Society 141:68–75.

Isaak, D. J., C. C. Muhlfeld, A. S. Todd, R. Al-Chokhachy, J. Roberts, J. L. Kershner, K. D. Fausch, and S. W. Hostetler. 2012. The past as prelude to the future for understanding 21st-century climate effects on Rocky Mountain trout. Fisheries 37:542–556.

Johnson, D. W., and K. Fite. 2007. The status of desert Redband Trout in southwestern Idaho. Pages 85–90 in M. J. Brouder and J. A. Scheurer, editors. Status, distribution, and conservation of native freshwater fishes of western North America. American Fisheries Society, Symposium 53, Bethesda, Maryland.

Kammerer, B. D., and S. A. Heppell. 2013. Individual condition indicators of thermal habitat quality in field populations of Redband Trout (*Oncorhynchus mykiss gairdneri*). Environmental Biology of Fishes 96:823–835.

Keleher, C. J., and F. J. Rahel. 1996. Thermal limits to salmonid distributions in the Rocky Mountain region and potential habitat loss due to global warming: a geographic information system (GIS) approach. Transactions of the American Fisheries Society 125:1–13.

Knudsen, K. L., C. C. Muhlfeld, G. C. Sage, and R. F. Leary. 2002. Genetic structure of Columbia River Redband Trout populations in the Kootenai River drainage, Montana, revealed by microsatellite and allozyme loci. Transactions of the American Fisheries Society 131:1093–1105.

Kozfkay, C. C., M. R. Campbell, K. A. Meyer, and D. J. Schill. 2011. Influences of habitat and hybridization on the genetic structure of Redband Trout in the upper Snake River basin, Idaho. Transactions of the American Fisheries Society 140:282–295.

Krueger, C. C., and B. May. 1991. Ecological and genetic effects of salmonid introductions in North America. Canadian Journal of Fisheries and Aquatic Sciences 48:66–77.

Li, H. W., G. A. Lamberti, T. N. Pearsons, C. K. Tait, and J. L. Li. 1994. Cumulative effects of riparian disturbances along high desert trout streams of the John Day basin, Oregon. Transactions of the American Fisheries Society 123:627–640.

May, B. E., and S. Albeke. 2005. Rangewide status of Bonneville Cutthroat Trout (*Oncorhynchus clarki utah*) 2004. Utah Division of Wildlife Resources, Publication 05-02, Salt Lake City.

May, B. E., W. Urie, and B. B. Shepard. 2003. Rangewide status of Yellowstone Cutthroat Trout (*Oncorhynchus clarki bouvieri*): 2001. Montana Department of Fish, Wildlife and Parks, Helena.

Meehan, W. R. 1991. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society, Special Publication 19, Bethesda, Maryland.

Meyer, K. A., J. A. Lamansky Jr., and D. J. Schill. 2010. Biotic and abiotic factors related to Redband Trout occurrence and abundance in desert and montane streams. Western North American Naturalist 70:77–91.

Meyer, K. A., D. J. Schill, E. R. J. M. Mamer, C. C. Kozfkay, and M. R. Campbell. 2014. Status of Redband Trout in the upper Snake River basin of Idaho. North American Journal of Fisheries Management 34:507–523.

Miller, R. R., J. D. Williams, and J. E. Williams. 1989. Extinction of North American fishes during the past century. Fisheries 14:22–38.

Mooney, H. A., and E. E. Cleland. 2001. The evolutionary impact of invasive species. Proceedings of the National Academy of Sciences of the USA 98:5446–5451.

Muhlfeld, C. C. 2002. Spawning characteristics of Redband Trout in a headwater stream in Montana. North American Journal of Fisheries Management 22:1314–1320.

Muhlfeld, C. C., D. H. Bennett, and B. Marotz. 2001a. Fall and winter habitat use and movement by Columbia River Redband Trout in a small stream in Montana. North American Journal of Fisheries Management 21:170–177.

Muhlfeld, C. C., D. H. Bennett, and B. Marotz. 2001b. Summer habitat use by Columbia River Redband Trout in the Kootenai River drainage, Montana. North American Journal of Fisheries Management 21:223–235.

Muhlfeld, C. C., S. T. Kalinowski, T. E. McMahon, M. L. Taper, S. Painter, R. F. Leary, and F. W. Allendorf. 2009. Hybridization rapidly reduces fitness of a native trout in the wild. Biology Letters 5:328–331.

Muhlfeld, C. C., R. P. Kovach, L. A. Jones, R. Al-Chokhachy, M. C. Boyer, R. F. Leary, W. H. Lowe, G. Luikart, and F. W. Allendor. 2014. Invasive hybridization in a threatened species is accelerated by climate change. Nature Climate Change 4:620–624.

Narum, S. R., N. R. Campbell, C. C. Kozfkay, and K. A. Meyer. 2010. Adaptation of Redband Trout in desert and montane environments. Molecular Ecology 19:4622–4637.

Narum, S. R., N. R. Campbell, K. A. Meyer, M. R. Miller, and R. W. Hardy. 2013. Thermal adaptation and acclimation of ectotherms from differing aquatic climates. Molecular Ecology 22:3090–3097.

Neville, H. M., and J. B. Dunham. 2011. Patterns of hybridization of nonnative Cutthroat Trout and hatchery Rainbow Trout with native Redband Trout in the Boise River, Idaho. North American Journal of Fisheries Management 31:1163–1176.

Pearse, D. E., S. L. Gunckel, and S. E. Jacobs. 2011. Population structure and genetic divergence of coastal Rainbow and Redband trout in the upper Klamath basin. Transactions of the American Fisheries Society 140:587–597.

Peterson, D. P., B. E. Rieman, J. B. Dunham, K. D. Fausch, and M. K. Young. 2008. Analysis of trade-offs between threats of invasion by nonnative Brook Trout (*Salvelinus fontinalis*) and intentional isolation for native Westslope Cutthroat Trout (*Oncorhynchus clarkii lewisi*). Canadian Journal of Fisheries and Aquatic Sciences 65:557–573.

Peterson, E. E., and J. M. Ver Hoef. 2010. A mixed-model moving-average approach to geostatistical modeling in stream networks. Ecology 91:644–651.

R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available: http://www.R-project.org./ (November 2014).

Rahel, F. J. 2000. Homogenization of fish faunas across the United States. Science 288:854–856.

Rhymer, J. M., and D. Simberloff. 1996. Extinction by hybridization and introgression. Annual Review of Ecology and Systematics 27:83–109.

Rieman, B. E., and J. D. McIntyre. 1995. Occurence of Bull Trout in naturally fragmented habitat patches of varied size. Transactions of the American Fisheries Society 124:285–296.

Rodnick, K. J., A. K. Gamperl, K. R. Lizars, M. T. Bennett, R. N. Rausch, and E. R. Keeley. 2004. Thermal tolerance and metabolic physiology among Redband Trout populations in southeastern Oregon. Journal of Fish Biology 64:310–335.

Schill, D. J., G. W. LaBar, E. R. J. M. Mamer, and K. A. Meyer. 2010. Sex ratio, fecundity, and models predicting length at sexual maturity of Redband Trout in Idaho desert streams. North American Journal of Fisheries Management 30:1352–1363.

Shepard, B. B., B. E. May, and W. Urie. 2005. Status and conservation of Westslope Cutthroat Trout within the western United States. North American Journal of Fisheries Management 25:1426–1440.

Simmons, R. E., P. Lavretsky, and B. May. 2010. Introgressive hybridization of Redband Trout in the upper McCloud River watershed. Transactions of the American Fisheries Society 139:201–213.

Small, M. P., J. G. McLellan, J. Loxterman, J. Von Bargen, A. Frye, and C. Bowman. 2007. Fine-scale population structure of Rainbow Trout in the Spokane River drainage in relation to hatchery stocking and barriers. Transactions of the American Fisheries Society 136:301–317.

Sprowles, A. E., M. R. Stephens, N. W. Clipperton, and B. P. May. 2006. Fishing for SNPs: a targeted locus approach for single-nucleotide polymorphism discovery in Rainbow Trout. Transactions of the American Fisheries Society 135:1698–1721.

Stearley, R. F., and G. R. Smith. 1993. Phylogeny of the Pacific trout and salmon (*Oncorhynchus*) and genera of the family Salmonidae. Transactions of the American Fisheries Society 122:1–33.

Tate, K. W., D. L. Lancaster, and D. F. Lile. 2007. Assessment of thermal stratification within stream pools as a mechanism to provide refugia for

native trout in hot, arid rangelands. Environmental Monitoring and Assessment 124:289–300.

Thurow, R. F., D. C. Lee, and B. E. Rieman. 1997. Distribution and status of seven native salmonids in the interior Columbia River basin and portions of the Klamath River and Great basins. North American Journal of Fisheries Management 17:1094–1110.

Thurow, R. F., B. Rieman, D. C. Lee, P. J. Howell, and R. D. Perkinson. 2007. Distribution and status of Redband Trout in the interior Columbia basin and portions of the Klamath River and Great basins. Pages 28–46 *in* R. K. Schroeder and J. D. Hall, editors. Redband Trout: resilience and change in a changing landscape. American Fisheries Society, Oregon Chapter, Corvallis.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. Science 277:494–499.

Wenger, S. J., D. J. Isaak, C. H. Luce, H. M. Neville, K. D. Fausch, J. B. Dunham, D. C. Dauwalter, M. K. Young, M. M. Elsner, B. E. Rieman, A. F. Hamlet, and J. E. Williams. 2011. Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. Proceedings of the National Academy of Sciences of the USA 108:14175–14180.

Williams, J. E., A. L. Haak, N. G. Gillespie, and W. T. Colyer. 2007. The conservation success index: synthesizing and communicating salmonid condition and management needs. Fisheries 32:477–492.

Williams, J. E., A. L. Haak, H. M. Neville, and W. T. Colyer. 2009. Potential consequences of climate change to persistence of Cutthroat Trout populations. North American Journal of Fisheries Management 29:533–548.

Williams, J. E., J. E. Johnson, D. A. Hendrickson, S. Contreras-Balderas, J. D. Williams, M. Navarro-Mendoza, D. E. McAllister, and J. E. Deacon. 1989. Fishes of North America endangered, threatened, or of special concern: 1989. Fisheries 14(6):2–20.

Zoellick, B. W. 1999. Stream temperatures and the elevational distribution of Redband Trout in southwestern Idaho. Great Basin Naturalist 59:136–143.

Zoellick, B. W. 2004. Density and biomass of Redband Trout relative to stream shading and temperature in southwestern Idaho. Western North American Naturalist 64:18–26.

Zoellick, B. W., D. B. Allen, and B. J. Flatter. 2005. A long-term comparison of Redband Trout distribution, density, and size structure in southwestern Idaho. North American Journal of Fisheries Management 25:1179–1190.

Zoellick, B. W., and B. S. Cade. 2006. Evaluating Redband Trout habitat in sagebrush desert basins in southwestern Idaho. North American Journal of Fisheries Management 26:268–281.